CHROMOSOME NUMBERS IN COMPOSITAE, XV: LIABEAE

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ABSTRACT

Limited but strategic knowledge of chromosome numbers in the small, mostly Andean tribe Liabeae includes records of 12 of the 16 genera: *Cacosmia* ($x = 7$); *Chionopappus* ($n =$ ca. 9); *Ferreyranthus*, *Oligactis*, and *Liabum* ($x = 18$); *Sinclairia* ($x = 16$); *Paranephelius* ($x = 9, 14$); *Pseudonoseris* ($n = 12$?); *Erato* ($x = 9$); *Philoglossa* ($n = 18$); *Chrysactinium* ($x = 12$); *Munnozia* ($n = 10, 11, x = 12$). The tribal base number is apparently $x = 9$ supporting a long, separate history from the diploid elements of Vernonieae ($x = 10$) in the Eastern Hemisphere. Apparent aneuploid series of the type seen in *Munnozia* are regarded as reductions from the highest number. No correlation is seen between chromosome number and habit in the tribe. All cytologically known elements of the tribe with extensive distribution beyond the ancestral Ecuadorian–Peruvian area are polyploid. Differences in chromosome number combined with geography provide almost complete generic isolation in the tribe, and no evidence is noted of hybridization between extant genera.

The present paper continues a series dealing with chromosome numbers of Compositae (Raven et al., 1960; Raven & Kyhos, 1961; Ornduff et al., 1963, 1967; Payne et al., 1964; Solbrig et al., 1964, 1969, 1972; Anderson et al., 1974; Powell et al., 1974, 1975; King et al., 1976; Tomb et al., 1978; Robinson et al., 1981) and is the first dealing with the elements of Liabeae as a united group recognized at tribal level. Because data for the tribe are limited, reports from the literature are included in the table with altered identifications where necessary. New reports are provided for 31 populations of 15 species including new reports for nine species and one genus (marked respectively in Table 1).

The new reports in this paper are based on material collected by R. M. King and counted by A. M. Powell and J. F. Weedin. The chromosome counts have been made from aceto-carmine or aceto-orceine squashes of microsporocytes in meiosis. Voucher specimens of the King collections are in US, a second set is in MO.

Robinson (1983a) recognized about 157 species of Liabeae in 15 genera; his paper is the basis for comparison in this paper. The subsequently described monotypic *Bishopanthus* of Peru (Robinson, 1983b) is unknown cytologically and will not be considered in the present study. In spite of the comparatively small size of the tribe, Liabeae show considerable diversity in many structural details (Robinson & Brettell, 1974) and pol-

len (Skvarla et al., 1977) which are used as the basis for three subtribes, Liabinae, Paranepheliinae, and Munnoziinae, in the recent revision by Robinson (1983a). Present information indicates that the chromosome base numbers in the tribe are also diverse. They correlate to a considerable extent with the revised generic concepts and show distinctive trends in different subtribes.

Previous records of chromosome numbers of Liabeae are scattered and often confusing. Ornduff et al. (1963) offer the only cytological evaluation of Liabeae as a group, but only those parts treated under the traditional concept as subtribe Liabinae in Senecioneae. The traditional disposition, derived from Bentham (1873) and Hoffmann (1894), was totally flawed by the inclusion of foreign elements such as *Neurolaena* and *Schistocarpha*, which are now placed in Heliantheae, by the exclusion of true members of Liabeae such as *Chionopappus*, *Cacosmia*, and *Philoglossa*, and by the placement of all remaining members of the tribe in a single genus, *Liabum*. Ornduff et al. (1963) were able to mention only one chromosome count of a true member of the tribe, a *Liabum* sp. (*L. ovatum* vel aff.) reported by Diers (1961) as $n = 14$. The chromosome counts available in the unnatural group were said by Ornduff et al. to "attest to the isolated position of the Liabinae."

A number of additional chromosome counts

TABLE 1. Chromosome numbers and sources for Liabeae.

Species	Chromosome Number (n)	Locality or Literature Source
Cacosmia rugosa H.B.K.	7 (possibly + 1 small fragment)[b]	Ecuador. Azuay: ca. 6 km SE of Cumbe, *King 6702*
	7 (bivalents all same size)[b]	Ecuador. Loja: 7 km W of Loja, *King & Almeda 7889*
Cacosmia rugosa var. *kingii* H. Robinson	7 + 1 small fragment[b]	Ecuador. Loja: ca. 2 km E of Loja, *King 6913*
	7 (bivalents all same size)[b]	Ecuador. Zamora-Chinchipe: 17 km E of Loja, *King & Almeda 7929*
Chionopappus benthamii S. F. Blake	ca. 9 ($2n = 18$–20)	Peru (Diers, 1961)
Chrysactinium hieracioides (H.B.K.) H. Robinson & Brettell	12	Peru (Turner et al., 1967; as *Liabum*)
	12	Peru (Dillon & Turner, 1982)
	12–14[a]	Ecuador. Loja: 2 km N of Chinchas, *King & Almeda 7962*
	ca. 12 possibly even 13 (or even 14, 15, 16)[a]	Peru. Cajamarca: 41 km NE of Cajamarca, *King & Bishop 9128*
	13 ± 1 (not clear)[a]	Peru. Amazonas: along road SE of Chachapoyas, *King & Bishop 9200*
	12 or 13 [in some cells seemingly clear $n = 12$; either $n = 12 + 1$ fragment or 13[II]; 1 very large bivalent (or multivalent?); large bivalent very clear in some cells][a]	Peru. Amazonas: 40 km SW of Leimebamba, *King & Bishop 9245*
	13 ± 1 (in some cells looks like $n = 12$ or $n = 12 + 1$ fragment; possibly 12, 13, or 14; heteromorphic bivalents make interpretation difficult; 1 large II and varying sizes down to small, some smaller ones even fragment-looking; bridge seen in few cells so larger "bivalent" possibly is a multivalent)[a]	Peru. Amazonas: 23 km S of Tingo, *King & Bishop 9273*
Chrysactinium rosulatum (Hieron.) H. Robinson & Brettell	12	Peru (Dillon & Turner, 1982; as *C. acaule*)
	13 or 14 [1 larger bivalent, 3 moderate-sized bivalents, other smaller bivalents (seemingly); heteromorphic bivalents make it difficult to interpret (possibly even $n = 12$[II])][a]	Peru. Cajamarca: 55 km NE of Cajamarca, *King & Bishop 9139*

TABLE 1. Continued.

Species	Chromosome Number (n)	Locality or Literature Source
Erato polymnioides DC.	9	Ecuador (Olsen, 1980; as Munnozia)
Erato vulcanica (Klatt) H. Robinson	9	Colombia. Putumayo (Jansen et al., 1984; as Liabum)
	9	Colombia (Olsen, 1980; as Munnozia)
	9	Colombia (Turner et al., 1979; as Liabum cf.)
Ferreyranthus rugosus (Ferreyra) H. Robinson & Brettell	ca. 18	Peru (Turner et al., 1967; as Liabum)
Ferreyranthus verbascifolius (H.B.K.) H. Robinson & Brettell	19 ± 1 (heteromorphic bivalents)[a]	Ecuador. Azuay: ca. 9 km N of Sigsig, King 6647
Liabum bourgeaui Hieron.	report of 9 believed in error (see text)	(Olsen, 1980)
Liabum eggersii Hieron.	ca. 20 + 1, 2 fragments[a]	Ecuador. Guayas: ca. 12 km SE of Vinces, King 7010
Liabum floribundum Less.	18	Peru (Dillon & Turner, 1982)
	19 + 2[a]	Ecuador. Tungurahua: 7 km E of Baños, King 6541
	ca. 20[a]	Ecuador. Azuay: ca. 14 km SW of Girón, King 6686
	19[a]	Ecuador. Azuay: ca. 5–6 km NE of Cuenca, King 6875
	19 + 6, 7 fragments[a]	Ecuador. Chimborazo: ca. 39 km NE of Bucay, King 6961
	ca. 19 [seemingly 19^{II} and 3 round fragments or I's; appear to be 17 major bivalents; these heteromorphic, with 2 of these smaller than all the others (interpreted as II's if $n = 19^{II}$) and precociously separating by metaphasis I][a]	Ecuador. Cañar: 67 km E of Cañar, King & Almeda 7795
Liabum kingii H. Robinson	17–20[a]	Ecuador. Tungurahua: ca. 2 km E of Río Negro, King 6555
Liabum melastomoides (H.B.K.) Less.	19[a]	Colombia. Valle del Cauca: Cordillera Central, vertiente occidental, piedemonte entre La Uribe y Astelia (Bugalagrande-Sevilla), Vuelta de Violín, Cuatrecasas & Cuadros 28932
Liabum subacaule Rydb.	18	Dominican Republic (Torres & Liogier, 1970)
Munnozia ferreyrii H. Robinson	12	Peru (Dillon & Turner, 1982)
Munnozia hastifolia (P. & E.) H. Robinson & Brettell	11 (with 1 large pair)[a]	Ecuador. Tungurahua: ca. 2 km E of Río Negro, King 6562
Munnozia jussieui (Cass.) H. Robinson & Brettell	12[a]	Ecuador. Pastaza: ca. 18 km N of Puyo, King 6569
	ca. 13	Ecuador (Jansen & Stuessy, 1980; as Liabum)
Munnozia lyrata (A. Gray) H. Robinson & Brettell	12	Colombia. Nariño (Jansen et al., 1984; as Liabum)
	ca. 24	Peru (Dillon & Turner, 1982)

TABLE 1. Continued.

Species	Chromosome Number (n)	Locality or Literature Source
Munnozia maronii (Andre) H. Robinson	12 + 1[a]	Bolivia. Cochabamba: 25 km from Colomi on road to Tunari, *King & Bishop 7687*
Munnozia senecionidis Benth.	10	Colombia (Powell & King, 1969; as *Liabum megacephalum*)
	10	Colombia. Cundinamarca (Jansen et al., 1984; as *Liabum sagittatum*)
	ca. 12[a]	Ecuador. Loja: ca. 8 km E of Loja, *King 6918*
	10 (8 normal-sized bivalents and 2 bivalents twice the normal size; the large bivalents possibly multivalents but behaving like bivalents)[a]	Ecuador. Azuay: 8–10 km S of Cumbe, *King & Almeda 7773*
	10 ? (same as *7773*, except that some of 8 smaller bivalents slightly heteromorphic. See text)[a]	Ecuador. Loja: 10 km S of Seraguro, *King & Almeda 7834*
	10 (same as *7834f*)[a]	Ecuador. Loja: 2 km E of Loja, *King & Almeda 7909*
Oligactis pichinchensis (Hieron.) H. Robinson & Brettell	ca. 39	Ecuador (Jansen & Stuessy, 1980; as *Liabum*)
Paranephelius jelskii (Hieron.) H. Robinson & Brettell	ca. 18	Colombia. Cundinamarca (Jansen et al., 1984; as *Liabum*)
	9	Peru (Turner et al., 1967; as *Liabum bullatum*)
Paranephelius ovatus Wedd.	14, 15[a]	Bolivia. Cochabamba: at Cholla, *King & Bishop 7540*
Paranephelius uniflorus P. & E.	14	Peru (Diers, 1961; as *Liabum ovatum* vel aff.)
Philoglossa peruviana DC.?	18	Peru (Diers, 1961; as *Philoglossa pterocarpha*)
Pseudonoseris szyszylowiczii (Hieron.) H. Robinson & Brettell	12 (questioned in text)	Peru (Dillon & Turner, 1982)
Sinclairia discolor Hook. & Arn.	17, 18	Mexico (Powell et al., 1974; as *Liabum*)
Sinclairia hypochlora (S. F. Blake) Rydb.	15 or 16 (n = 15 with one large bivalent or n = 16; bivalents heteromorphic and abnormal)[a]	Guatemala. Suchtepequez: ca. 30 km W of Mazatenango, *King 7245*
Sinclairia sublobata (B. L. Robinson) Rydb.	15, 16 (n = 15 with one bivalent extra large, or n = 16, or possibly even n = 17)[a]	Guatemala. Escuintla: ca. 22 km SW of Amatillán, *King 7171*
	16 (multinucleolate, 1 large, 1–3 smaller; appears to be n = 15, 16 pairs at diakinesis not forming characteristic shapes; bivalents different size)[b]	Guatemala. Quezaltenango: ca. 18 km S of Quezaltenango, *King 7258*

[a] New reports.
[b] First report for genus.

have become available for the group since the earlier summary, some as a result of recognition of the previously reported *Philoglossa* and *Chionopappus* (Diers, 1961) as members of the tribe, others as a result of new reports. Nordenstam (1977), in his short summary of the tribe, cited chromosome numbers for seven genera. Dillon and Turner (1982) gave reports for four genera.

The few reports in recent years by other authors, and the reports in the present study are still limited in number, but the total is now sufficient to see some patterns in the tribe that have not been evident before. The rather complete understanding of the tribe on the basis of other characters (Robinson, 1983a; Robinson & Marticorena, unpubl. data) has aided further and provides a basis for important phyletic conclusions.

The reports in the present paper represent a small return on many attempts. The members of the Liabeae are much less easily counted than most members of such tribes as the Eupatorieae (King et al., 1976) or Heliantheae (Robinson et al., 1981). However, the various ways in which chromosomes are difficult to count are themselves characters worthy of study, and are often characteristic of genera or tribes. One example in the subfamily Asteroideae (sensu Robinson, 1977) is *Mikania* in the normally rather easily counted Eupatorieae. *Mikania* seems to have some variation in the actual number of chromosomes, but the primary difficulty lies in the slight differential in the stainability of the chromosomes and the cytoplasm. The chromosomes stain poorly and the cytoplasm takes enough stain to make the chromosomes difficult to count. Most of the examples of less easily counted Asteraceae, however, are in Cichorioideae (sensu Robinson, 1977) in which Liabeae is included. Collections of Mutisieae, Vernonieae, and Liabeae all seem to yield characteristically poor results.

The comparison of this feature that is particularly important is that between Liabeae and Vernonieae, because the former have often been included in the latter in spite of their opposite leaves, rays, yellow corollas, and frequent milky sap (Cassini, 1823, 1825, 1830; Nash, 1976; Jansen & Stuessy, 1980). That both tribes have chromosomes that are difficult to count might be taken as an indication of relationship, but according to the observations by Powell, the nature of the problem in the two tribes is not the same. In Liabeae there are uncertainties in the interpretation of heteromorphic bivalents that appear to occur in many of the genera (e.g., *Chrysactinium*, *Liabum*, *Munnozia*). When the heteromorphic meiosis I configurations occur, one or two of them appear to be much larger bivalents (or multivalents?), and then the other bivalents occur in varying sizes down to small, with some of the smaller configurations often resembling fragments in size and shape. When bud material is adequate it is often possible to resolve uncertain counts by observing meiotic chromosome behavior through several stages. In Liabeae, however, aceto-carmine staining is often poor at prophase I stages before and through diakinesis. Metaphase I and anaphase I chromosomes usually stain deeply with aceto-carmine. In Vernonieae, aceto-carmine preparations often reveal poorly stained bivalents that remain clumped or "sticky" in meiosis I stages. According to Sterling Keeley (pers. comm.), Vernonieae yield better results when collected at midday, a trait not tested for in Liabeae.

CYTOLOGICAL EVIDENCE REGARDING ORIGINAL CHROMOSOME NUMBER AND RELATIONSHIPS

In many tribes in the Asteraceae, original base numbers have been determined with reasonable confidence (Senecioneae—Ornduff et al., 1963; Eupatorieae—King et al., 1976; Heliantheae—Robinson et al., 1981). The various chromosome numbers known for Liabeae are adequate for a similar determination for that tribe.

There have been various proposals of a base number for the Asteraceae, but only two are regarded here as credible. The number $x = 9$ with its multiples is most common in the family (Solbrig, 1977) and has been suggested as the base number for the family by Raven (1975). More recently, Robinson et al. (1981) have suggested $x = 10$ as a base number for at least the entire subfamily Asteroideae. Evidence of predominant decreasing aneuploidy in Asteraceae would favor $x = 10$ as ancestral in most Cichorioideae as well. Still, internal evidence from Liabeae does not fully agree with the external evidence. The most common chromosome numbers in the tribe seem to be $n = 9$ and $n = 18$ or ca. 18. The counts of $n = 9$ seem centrally located in the tribe and have been cited from elements of all three subtribes. The number $n = 10$ is reported, perhaps
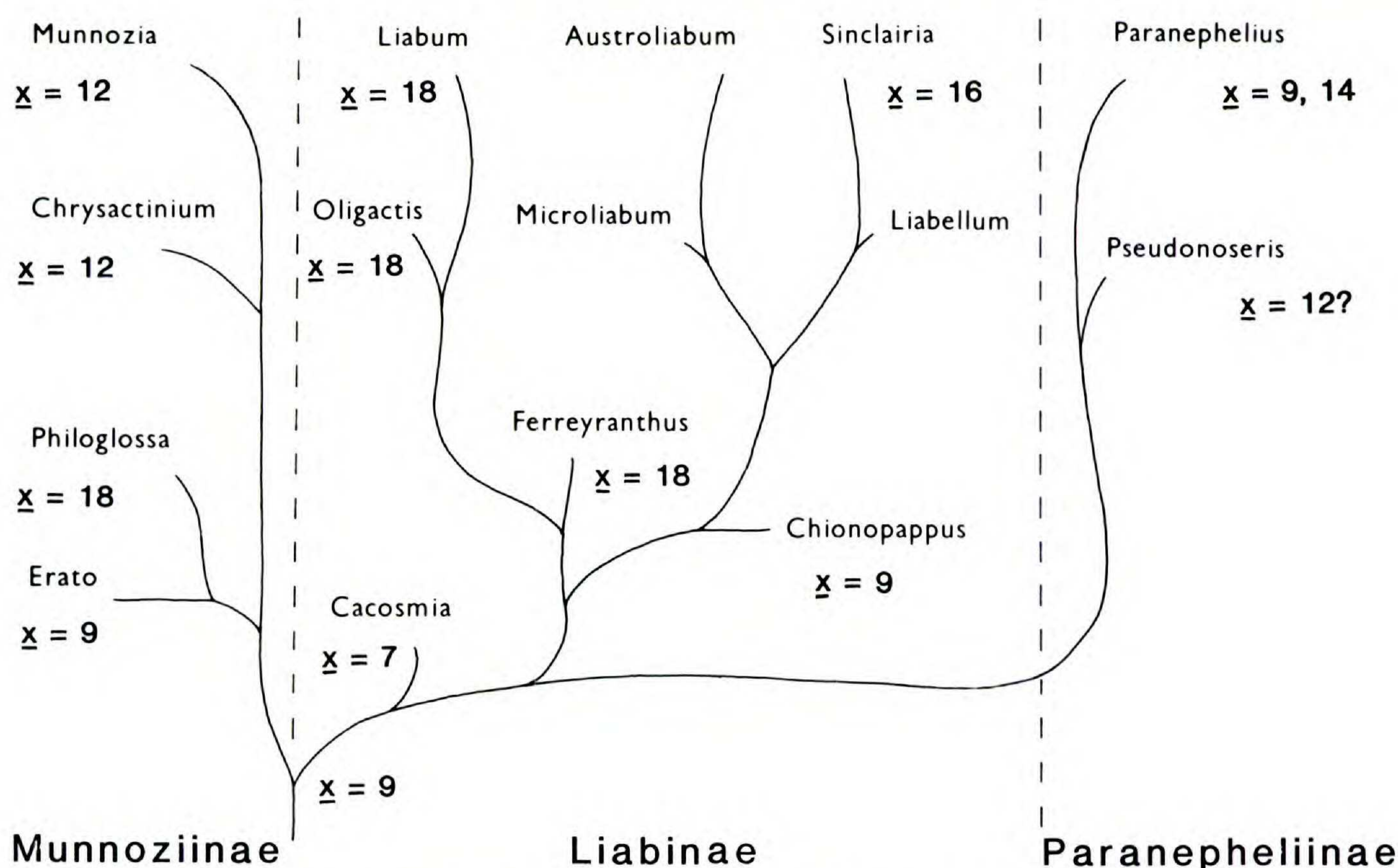
FIGURE 1. Schematic representation of possible relationships of genera and subtribes of the Liabeae (from Robinson, 1983a) with postulated basic chromosome numbers inserted.

erroneously, in *Munnozia* but in a comparatively specialized element of that genus (Robinson, 1983a) as explained below. A base of $x = 9$ would explain adequately all the elements of the Liabeae, and there is no need to assume a higher base of $x = 10$ within the reconstructible history of the tribe. No evidence of an ancestral $x = 10$ survives in extant Liabeae.

The basic chromosome number in Liabeae and the pattern of variation in chromosome numbers both furnish significant contrasts from other elements of the family which have been considered related. The base of $x = 9$ and the lack of stability in the chromosome number in the tribe contrast with the nearly consistent $n = 10$ of Senecioneae in which members of the Liabeae were traditionally placed (Bentham, 1873; Hoffmann, 1894). This provides some additional support for the removal of Liabeae from the Asterioidean Senecioneae, which has been proposed by numerous recent workers (Robinson & Brettell, 1974; Wagenitz, 1976; Nordenstam, 1977; Nash, 1976; Jansen & Stuessy, 1980; Robinson, 1983a).

Most of these recent workers place Liabeae near or in Vernonieae in the series of tribes presently included in the expanded Cichorioideae (or a segregate group Vernonioideae Turner ex Jansen & Stuessy, 1980). It is Vernonieae to which

Liabeae have closest resemblance in the general aspect of their styles, anthers, and pappus. The base number of either $x = 9$ or 10 suggested by Jones (1977) for Vernonieae, refined to a probable $x = 10$ by Robinson et al. (1981), is not significantly different from that in Liabeae. Nevertheless, actual relationships between the two tribes may not be as direct as many authors suppose, since there are significant differences in morphological, anatomical, and palynological characters. A more careful analysis of the cytology reveals an important discrepancy between the tribes in chromosomes as well. In the Vernonieae, the $x = 10$ is characteristic of the Paleotropical elements and various specialized elements that evidently recently dispersed from that area (Jones, 1977). In contrast, the Neotropical elements, that overlap geographically with Liabeae, have chromosome numbers of $x = 19$ (Funk in Turner, 1981) and $x = 17$ derived from polyploids of $x = 10$. On the basis of present evidence, $n = 10$ is not represented in the basically American elements of the Vernonieae. This raises the possibility that the Vernonieae were originally restricted to the Paleotropical Region and were initially introduced into the Western Hemisphere in a polyploid condition.

Liabeae are strictly Andean in origin, with a

series of chromosome numbers that seem to be based on an original $x = 9$. These numerical and geographical discrepancies, correlated with morphological, anatomical, and palynological discrepancies (Robinson, 1983a; Robinson & Marticorena, unpubl. data), suggest that the two tribes had separate origins in separate hemispheres and that their common ancestor is quite remote.

REVIEW OF THE CHROMOSOME NUMBERS

The following discussion of chromosome numbers in Liabeae follows the three subtribal groupings of Robinson (1983a). For purposes of orientation, it should be noted that according to Robinson, Liabinae and Munnoziinae appear to represent a basal divergence in the tribe, and Paranepheliinae seem to have arisen from slightly more advanced members of Liabinae. As such, all three subtribes contain elements showing comparatively primitive characters.

LIABINAE

As shown below and in Table 1, and as summarized in Figure 1, genera of the subtribe fall into two groups. The first has chromosome numbers apparently consistently at $n = 7$ or 9, and the second has numbers apparently consistently near $n = 16$ or 18. The latter group includes all of the more widely distributed and more richly speciated genera of the subtribe.

A series of new reports clearly establishes $x = 7$ as the chromosome number for *Cacosmia*, and it is the only known occurrence of the number in the tribe. It is not difficult to interpret $x = 7$ as a reduction from $x = 9$ that seems basic in the tribe, although *Cacosmia* is a shrub, and such reduction usually involves reduction in the habit to less woody or shorter-lived plants (Bennett, 1972; Robinson et al., 1981). The primary traditional distinction of *Cacosmia*, the lack of the pappus, along with such features as the ranked involucral bracts and the modified arrangement of thickenings in the endothecial cells (Robinson, 1983a) do not justify placement in a separate tribe such as the Helenieae (Bentham, 1873) but do indicate some phyletic distance. The genus can be interpreted as one of the earliest divergences from the basal stock of the subtribe with a unique cytological history. Overwhelming evidence from other tribes and from other Liabeae against a base of $x = 7$ and against frequent aneuploid increase (Robinson et al., 1981) prohibits the acceptance of $x = 7$ as the forerunner of $x =$

9 in Liabeae. Furthermore, some specialized aspects of *Cacosmia* discourage any thought of a direct connection between the $x = 7$ of *Cacosmia* and the $x = 12–14$ of various Munnoziinae and Paranepheliinae.

Chionopappus of coastal Peru has been reported to have $n = $ ca. 9 by Diers (1961), and this is the only report of the supposed tribal base number in Liabinae. The genus is distinguished by its uniseriate plumose pappus and was originally placed in Mutisieae (Bentham, 1873). Other features of *Chionopappus*, however, are not unusual for Liabinae. The $n = 9$ in the genus indicates a point of origin in the subtribe before the incidence of polyploidy that characterizes the advanced genera, a point similar to the ones at which *Cacosmia* and the Paranepheliinae may have diverged.

The remaining known chromosome numbers in Liabinae are apparently at the polyploid level. In *Ferreyranthus* of Peru and southern Ecuador, there are reports of $n = 18$ or 19 plus or minus 1 on the basis of two closely related species. In this genus, polyploidy is associated with the most subarborescent members of the tribe, but the habit difference from genera such as *Cacosmia* is not sufficiently marked to indicate any particular correlation with polyploidy. There is no reason to assume that polyploidy in *Ferreyranthus* is anything but a part of the general polyploid trend in the more advanced members of Liabinae.

The majority of the chromosome reports from the subtribe are from *Liabum* and *Oligactis*. The two genera are centered geographically in the Andes of Colombia and Ecuador, but *Liabum* has attained the widest range of any genus in the tribe, from central Mexico and the Greater Antilles to Bolivia. The various reports indicate a chromosome number of $n = 18$ or 19. Because of the difficulties in counting chromosomes in the tribe, it is uncertain whether the variety in reports represents a true variety in numbers. The presence of a probable base of $x = 9$ in the tribe causes the present authors to favor $x = 18$ as basic for *Liabum, Oligactis,* and *Ferreyranthus.* The $n = $ ca. 39 reported from *Oligactis pichinchensis* indicates a further level of polyploidy in the group.

The report of $n = 9$ for *Liabum bourgeaui* by Olsen (1980) is anomalous in view of all other evidence for the generic group. Also, the species occurs in Mexico and Central America, but not in Colombia from where the collection is cited. The voucher from SWMT is actually *Verbesina*

barragana Cuatrecasas or a closely related species, which casts total doubt on the report because $n = 9$ is not characteristic of either genus. Unfortunately there are no other reports for *L. bourgeaui* or of its two closest relatives, *L. asclepiadeum* Schultz-Bipontinus of the northern Andes or *L. ferreyrii* H. Robinson of Peru.

The *Sinclairia* group of Mexico and Central America has been reported as $n = 17, 18$ by Powell et al. (1974) and Nordenstam (1977) on the basis of a single count of *S. discolor*. It seems notable that this report was uncertain toward a lower number from $n = 18$ because the present study shows $n = 15, 16$ for the genus on the basis of a number of species with one apparently clear count of $n = 16$. In the absence of better evidence, the $x = 16$ is regarded here as basic for the group.

Sinclairia, Ferreyranthus, and the genus-pair *Liabum* and *Oligactis* all have higher numbers of chromosomes presumably derived from polyploidy, but these comparatively advanced members of the subtribe may not share the same polyploid ancestry. Certainly, *Sinclairia* has structural features and latex that suggest closer relationship to *Chionopappus* with $n = $ ca. 9 than to the other polyploid genera.

PARANEPHELIINAE

The subtribe contains *Paranephelius* and *Pseudonoseris*. As can be seen in the table, there are only three chromosome number reports for *Paranephelius* showing two basically different numbers. The new report of $n = 14$ or 15 for *Paranephelius ovatus* supports the report of $n = 14$ ($2n = 28$) by Diers (1961: 465), although Diers's report for *P. ovatus* vel aff. from coastal Peru probably represents the closely related *P. uniflorus* Poepp. & Endl. At the same time, the $n = 9$ reported by Turner et al. (1967) for *P. jelskii* (as *P. bullatus*) fits well into the concept of $x = 9$ as a base for the tribe and is reported from the most divergent element in the genus. The element for which this ancestral number is reported is restricted in distribution in Amazonas in northern Peru while the probable derived group with $n = 14$ is widely distributed from more coastal northern Peru south to Bolivia and northernmost Argentina. These counts do not provide a basis for much speculation on the actual origin of the $n = 14$, but some numbers in the $n = 11$, 12 range occur in the *Munnozia* element of the Munnoziinae where possible patterns in the or-

igin of such aneuploid increases are discussed more fully.

The recent report of $n = 12$ from *Pseudonoseris szyszylowiczii* (Dillon & Turner, 1982) seems somewhat anomalous and needs confirmation. As reported, the number would represent an additional aneuploid increase in the subtribe separate from that cited above within *Paranephelius*. We hesitate to accept the present report because the voucher from F, collected 5 Jan. 1979, and a duplicate at US, while correctly determined, show only mature heads, a condition, which according to R. M. King is typical of the species at that time of year. It seems possible that the buds counted might have come by error from some intermixed *Munnozia* or *Chrysactinium* in which the number $n = 12$ is common.

MUNNOZIINAE

The subtribe contains four genera that fall easily into two groups, *Erato–Philoglossa* and *Chrysactinium–Munnozia*, on the basis of pubescence, endothecial cell structure, and pollen structure (Robinson, 1983a; Robinson & Marticorena, unpubl. data). Chromosome reports in Table 1 and the summary in Figure 1 show that the two groups are distinct cytologically also.

Erato and *Philoglossa* have ranges that broadly overlap in the central Andes south to Bolivia, but *Erato* is concentrated in the main Andean chains that reach north to Venezuela and Colombia with an extension to Costa Rica, whereas four of the five species of *Philoglossa* are restricted to the coastal ranges of Peru. The two genera have been placed in separate tribes in the traditional systems of classification of Bentham (1873) and Hoffmann (1894), although they prove intimately related on the basis of all characters except their pappus. The two genera share most notably a stiff type of vegetative hair, short, transversely polarized endothecial cells, a reduced number of ribs on the achene, a somewhat irregularly spinulose pollen, and a chromosome number based on $x = 9$. *Philoglossa* is generally more advanced in its more reduced pappus and its two rather than four ribs on the achene. Reports by Turner et al. (1979), Olsen (1980), and Jansen et al. (1984) firmly establish $n = 9$ as the number for *E. vulcanica*. Unfortunately, a number of attempts to count the closely related *E. polymnioides* DC. during the present study have failed, but one count of $n = 9$ has been provided by Olsen (1980). The report of $n = 18$ for *Phil-*

oglossa stenocarpa by Diers (1961) fits well with the $n = 9$ reported from the closely related *Erato*. The limited examples give little indication of the full distribution of polyploidy in the two genera; nevertheless, the polyploidy in the smaller though not necessarily more herbaceous *Philoglossa* is still another example of the lack of correlation between habit and chromosome number in the tribe.

Chrysactinium and *Munnozia* also have geographic ranges that overlap in the Andes of Ecuador and northern Peru, but the latter, larger genus extends much more widely to Costa Rica, Venezuela, and Bolivia. The two genera share a tomentose type of vegetative pubescence, vertically or obliquely polarized endothecial cells, usually ten-ribbed achenes, pollen with regularly distributed spinules, and chromosome numbers of $n = 10$ to ca. 13. *Chrysactinium hieracioides* now has many reports by Turner et al. (1967), Dillon and Turner (1982), and the new reports (see Table 1) indicate a chromosome number of $n = 12$, the same number reported from the Peruvian species *C. rosulatum* (as *C. acaule*, Dillon & Turner, 1982). The new report of $n = 13, 14$ in *C. rosulatum* (see Table 1) and reports of possible $n = 13$ in *C. hieracioides* may or may not represent true variation in the genus, but the reports of $n = 12$ seem more reliable, and that number also seems basic in the closely related *Munnozia*. In the examination of the King collections of *Chrysactinium* from Peru (*9128, 9139, 9200, 9245, 9273*), Powell noted a uniformity of karyotype that contrasted with that of a *Ferreyranthus* studied with uncertain results at the same time.

In *Munnozia*, most reports are based on *M. senecionidis* and indicate a chromosome number of $n = 10$ or 11. There is one report of $n = $ ca. 12 (see Table 1). However, on the basis of the drawings provided (Figs. 2, 3), Strother (pers. comm.) suggests the report of $n = 10$ is in error. He suggests that the cell illustrated in Figure 2 exhibited $8_{II} + 2_{IV}$ for $2n = 24$ or $10_{II} + 1_{IV}$ for $2n = 24$. This presumes that the larger configurations noted by Powell are actually multivalents even though they exhibited meiotic behavior that is characteristic of bivalents. Other species representing the great diversity of the genus, including *M. jussieui* (Jansen & Stuessy, 1980), *M. lyrata* and *M. ferreyrii* (Dillon & Turner, 1982), and *M. hastifolia* and *M. maronii* reported here, show mostly $n = 12$ or ca. 13 or $n = $ ca. 24, which
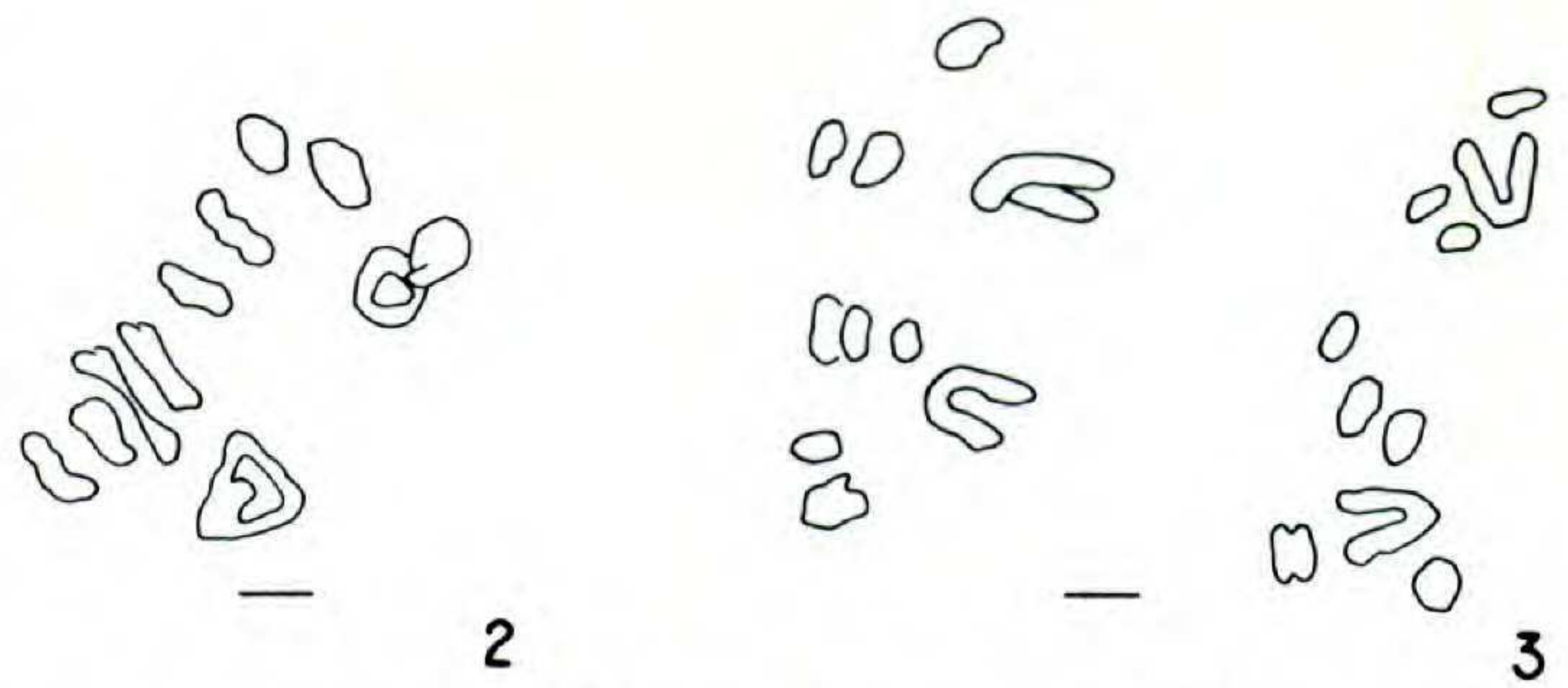
FIGURES 2, 3.   *Munnozia senecionidis* Benth. *King and Almeda 7834.*—2. Metaphase I.—3. Anaphase II. Line = 4 μm.

agrees more with *Chrysactinium*. On this basis we regard $x = 12$ as basic for the generic pair.

The $x = 12$ of the *Chrysactinium–Munnozia* group and the $x = 14$ of typical *Paranephelius* appear to be two clear examples of aneuploid gain in Liabeae in spite of the evidence from other groups such as Heliantheae (Robinson et al., 1981) regarding the comparative rarity of such gains in chromosome number. We have no inclination to regard either number as the result of polyploidy from numbers lower than $n = 9$, and neither group shows any evidence of close relationship to the one genus in the tribe, *Cacosmia*, having a chromosome number less than $n = 9$. As already indicated, there is also no close relationship between the *Munnozia* group and *Paranephelius*, and the two examples of aneuploid gain are thus totally independent. There is, however, no need to accept more than one instance of aneuploid gain in *Munnozia*. The series of numbers in *Munnozia* is at best a downward series that occurs in a specialized element of the genus. The $n = 12$ is basic to both genera and is obviously ancestral in the group. The occasional reports of still higher numbers in the *Munnozia* group might indicate that the ancestral number of the generic pair was actually higher than $n = 12$. Although no direct evidence is available, the apparent increasing aneuploidy might derive from some extinct polyploid ancestor having $n = 18$.

It is notable that series of numbers above the ancestral base number similar to those in *Munnozia* can be found in other tribes of Asteraceae. One such example is in the *Microspermum–Stevia–Piqueria* relationship of Eupatorieae. At present we favor an interpretation of that series like that of *Munnozia* with the highest number in the series being the first, followed by reduction. We suspect that many other seeming series of aneuploid increases should be interpreted in this way.

GENERAL CONCLUSIONS

Given the overall pattern of chromosome numbers in the Liabeae, there remain two general points of interest to be discussed.

The foregoing discussion of the genera and subtribes includes mention of many examples of polyploidy in the tribe, mostly concentrated in two series of advanced members of Liabinae. There seems to be an unusual lack of correlation of chromosome number with habit in the tribe, with little tendency for lower numbers in shorter-lived or more herbaceous plants as commonly occurs in other tribes (King et al., 1976; Solbrig, 1977) and in many other groups of plants. However, the polyploids in Liabeae do include all the elements that have their primary ranges north of the Ecuadorian–Peruvian center of the tribe. It is as though the diploid members of the tribe were restricted to their ancestral area, and only polyploids were able to invade new territories. This provides the possibility of an interesting test. Among the genera not yet counted is *Austroliabum,* a genus that has exceeded the ancestral range of the tribe to the south in Bolivia and Argentina. If the hypothesis is correct, then this genus should also be polyploid.

It has been observed (Robinson, 1983a) that intergeneric hybridization has left its mark on many of the large tribes of Asteraceae and may be an important factor in their success. However, there is no evidence of such hybridization in the Liabeae, and it has been suggested that this is correlated with the comparatively restricted size and distribution of the tribe. The present genera of Liabeae that are not geographically isolated tend to have different chromosome numbers, which would inhibit hybridization. The number of different basic numbers represented is remarkable considering the small number of extant genera (Fig. 1). From a cytologically uniform group of ancestors, *Cacosmia* can be seen as an early drop-out with reduction of its chromosome number to $n = 7$, whereas other genera became isolated by various higher chromosome numbers or by geography.

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